

Does the California market squid (*Loligo opalescens*) spawn naturally during the day or at night? A note on the successful use of ROVs to obtain basic fisheries biology data

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The California market squid (*Loligo opalescens* Berry), also known as the opalescent inshore squid (FAO), plays a central role in the nearshore ecological communities of the west coast of the United States (Morejohn et al., 1978; Hixon, 1983) and it is also a prime focus of California fisheries, ranking first in dollar value and tons landed in recent years (Vojkovich, 1998). The life span of this species is only 7–10 months after hatching, as ascertained by aging statoliths (Butler et al., 1999; Jackson, 1994; Jackson and Domier, 2003) and mariculture trials (Yang, et al., 1986). Thus, annual recruitment is required to sustain the population. The spawning season ranges from April to November and spawning peaks from May to June. In some years there can be a smaller second peak in November. In Monterey Bay, the squids are fished directly on the egg beds, and the consequences of this practice for conservation and fisheries management are unknown but of some concern (Hanlon, 1998). Beginning in April 2000, we began a study of the *in situ* spawning behavior of *L. opalescens* in the southern Monterey Bay fishing area.

The prevailing thought is that the majority of spawning activity takes place at night because fishermen have observed these squids mating under their bright lights (which are used to

attract and capture squids) and because television documentaries have revealed mating and spawning activity in large aggregations at night. The scientific literature on reproductive behavior is sparse. There are some cursory observations of actively spawning *L. opalescens* during diver surveys of egg beds (McGowan, 1954; Fields, 1965; Hobson, 1965; Hurley, 1977). Some daytime spawning has been seen both in southern and northern California but Fields (1965) and Hixon (1983) suggested indirectly that most spawning occurs at night. Shimek et al. (1984) also suggested night spawning by *L. opalescens* in Canada. Other loliginid squids whose natural behavior has been studied in the field were found to be daytime spawners (e.g., *L. pealeii*, *L. vulgaris reynaudii*, *Sepioteuthis sepioidea*; summarized in Hanlon and Messenger, 1996).

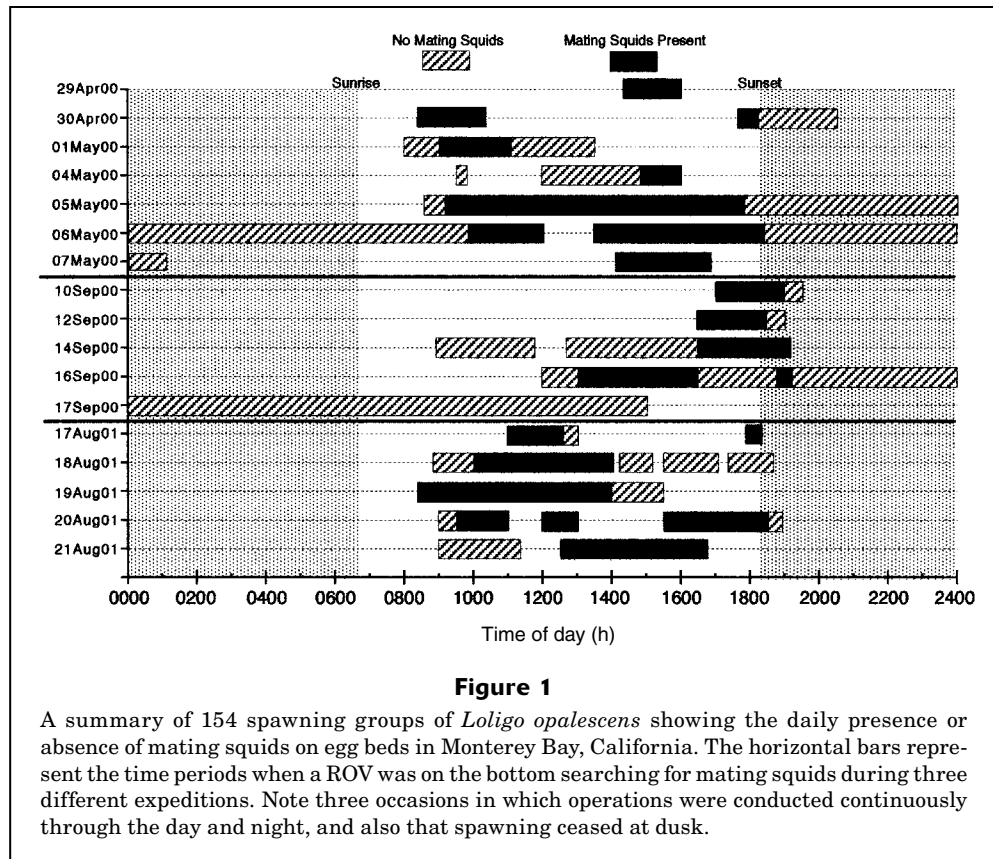
To help resolve this issue, we conducted three field expeditions (28 April–8 May 2000, 10–17 September 2000, and 16–21 August 2001) using remotely operated vehicles (ROVs) deployed either from the RV *John Martin* (Moss Landing Marine Laboratory) or the commercial squid FV *Lady J*. The ROVs were tethered vehicles with on-board video cameras and lights. Live video signals were transmitted by the tether to shipboard VCRs where

observational data were viewed and recorded. For the first field trip, a large S4 Phantom ROV was used; it was outfitted with a video camera and zoom lens with tilt capability, and the video was recorded on Hi8 format video decks. For the second and third trips, a smaller S2 inspection-class Phantom ROV on loan from the NOAA Sustainable Seas Expeditions was used; this ROV had a customized fiber-optic tether and the video data were recorded on mini-digital video cassettes. Our goal was to make ROV dives each day from approximately dawn to dusk and to make a few comparable all-night surveys. A combination of adverse weather conditions and technical problems with the ROVs rarely allowed continuous video observations. During dives, if squids were encountered, we used video to conduct focal animal samples on females (which were paired) for as long as squids were present, or as long as we could keep track of the same individuals. Unless absolutely necessary to see the squids (for instance at night or at depths greater than 30 m in turbid daytime conditions), lights were not used for video taping in an effort to minimize their impact on the mating squids. Squids acclimated within minutes to the ROVs. After the expeditions, the videotapes were studied and the behavioral and biological data were quantified on a multimotion playback VCR.

By “mating” we refer to the peculiar mating behavior of this species that is unique among loliginid squids. The male firmly grasps the female from her ventral side and holds her for minutes or hours in a “copulatory embrace” in a nearly vertical position. Both copulation (i.e., transfer of spermatophores) and deposition of egg capsules occur in this posture. For example, as the female exudes a new egg capsule, the male and female lower themselves in unison to the egg bed where the female deposits the egg capsule in the sand. We have reported elsewhere on egg-

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laying frequency (Hanlon et al., in press). Only very rarely did we observe females laying eggs while unattended by a male; in these cases the female was moribund and laying her last few egg strands.

Results and discussion

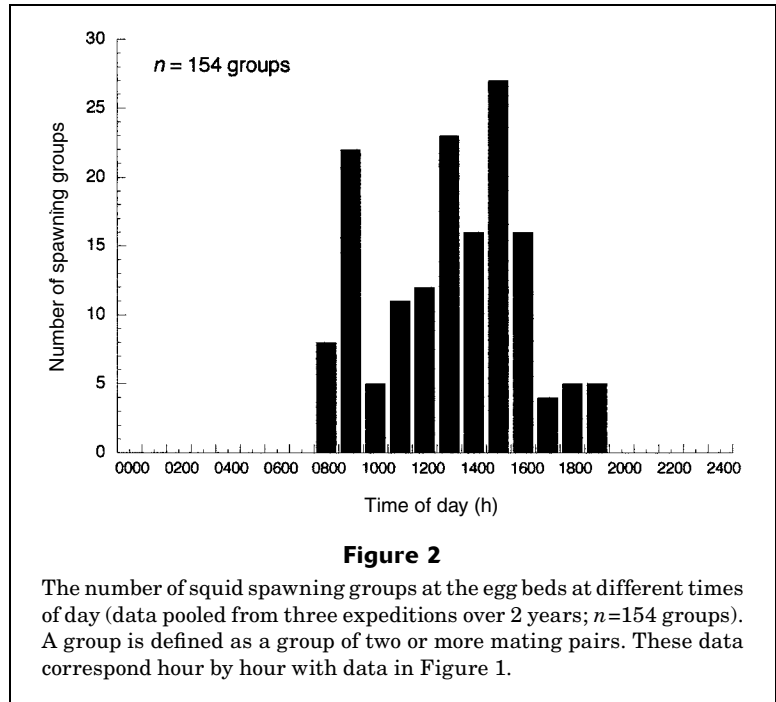
We examined 28 hours of videotape recorded during 50 ROV dives over 18 days (divided into three expeditions). Figure 1 illustrates the relative presence or absence of mating *Loligo opalescens* throughout 24-hour periods. The large gaps in the daytime observation record were due to ROV problems. Although observation times varied daily, it is clear that normal mating and egg-laying behaviors were exclusively observed during daylight hours (ca. 0800–1800 hours but with some seasonal variation) and concluded near dusk. In all instances in Figure 1 where egg-laying extended into the early evening, these mating assemblages had formed during daylight hours and persisted slightly past sunset and the number of participating squids constantly decreased as sunset approached and passed. Observations were made throughout the night on three nights. Not only were no mating squids ever encountered around the egg beds at night, but generally no squids were encountered at all near the seabed, despite large aggregations that were present higher in the water column. Thus the 200–400 watt lights on the ROVs never

induced any artificial spawning behavior because there were no squids present.

Figure 2 provides some quantification of Figure 1. This graph is based on 154 spawning groups that were videotaped and includes all three trips as well as the three “all night observations” illustrated in Figure 1. We were studying discrete groups of squids to examine mating dynamics and thus were sometimes biased to smaller groups of squids that could be kept in view. Overall, we observed that squids were present in greatest numbers in mid to late afternoon and absent during the night.

Our findings strongly indicate that the extensive egg beds produced at depths of 20–60 m in southern Monterey Bay (just beyond the kelp beds) are the result of daytime aggregations of mating *Loligo opalescens*. These benthic aggregations begin forming in the early morning hours and tend to be larger in the afternoon. Reproductive activity begins to wane toward sunset and comes to a near halt at sunset. We could find no evidence that egg laying occurs naturally during the night. All observations that we are aware of (mainly television documentaries) have occurred in the presence of artificial light sources near the surface provided either by fishermen or cinematographers. In the absence of artificial lighting, *L. opalescens* in South Monterey Bay does not aggregate into mating and spawning groups at night. Thus, we conclude that all significant egg deposition in the Monterey Bay fishery is the result of daytime aggregations of squids.

Two other ascribed characteristics of *L. opalescens* spawning are mass aggregations at the sea floor and subsequent die-offs after squids have spawned. Mass aggregations can be detected by standard fathometers used by commercial fishermen, who report that mass aggregations on the sea floor are rare in Monterey Bay. During our ROV operations we encountered only one large aggregation, which occurred on 21 August 2001. We estimated from our video recordings that there were approximately 3000–4000 squid in a 50-m² area on the sea floor and that intermittent egg laying was occurring over an area of ca. 2000 m² during a period of about 3 hours. Collectively, then, we recorded 154 very small spawning groups and one large spawning group. There was no mass die-off during or after this large spawning aggregation. Instead, we consistently observed in all spawning groups that females actively broke the embrace of the paired male and jetted strongly upwards away from the spawning groups and rejoined large schools in the upper water column. Thus, squids that dispersed from the egg beds were consistently in excellent condition—certainly not senescent or moribund. These observations corroborate the results of other studies on loliginid squids that spawn intermittently (Moltschaniwskyj, 1995; Maxwell and Hanlon, 2000). Twice we encountered large numbers of dead squids on the sea floor in the early morning, but in both instances the squid fishing fleet had been working in the same area the night before and it appeared as though these mortalities were associated with the purse-seine fishery; there were few eggs in those localities. McGowan (1954), Hobson (1965), and Cousteau and Dirole (1973) reported that squids died after spawning in S. California. Various *Loligo* spp. are noted for flexible reproductive strategies (*cf.* Hanlon and Messenger, 1996) so it should not be surprising if *L. opalescens* occasionally engaged in large reproductive events. Our data suggest that small groups of squids (20–200 individuals) generally descend during the day and lay eggs for several hours before rejoining squids in the water column. We encourage other researchers to use ROVs or SCUBA without lights and with stealthy approaches to determine the natural diurnal spawning of *L. opalescens* throughout its range. Given our findings that active sexual selection processes are occurring during the day and that there is vertical migration between the large schools of squid in the water column and the small spawning groups at the substrate, it would be prudent, at the very least, to restrict daytime fishing directly over egg beds or to create protected spawning areas in southern Monterey Bay. This strategy would allow the complex mating system of *L. opalescens* to be played out without direct disruption by fishing activity. In such a short-lived species, annual recruitment to the population is necessary; thus sufficient eggs must be laid for each new generation to ensure a viable living resource.



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